A PHYLOGENETIC ANALYSIS OF POECILIA

Abstract

Eleven species of the genus Poecilia, representing former supra-specific taxa, are compared with species formerly considered related in a phylogenetic analysis. Previous non-cladistic, superficially cladistic and fully cladistic classifications are discussed prior to the analysis, and some are compared to the phylogeny analyzed herein. Former supra-generic classifications are confirmed, whereas the analysis resulted in a partly resolved phylogeny, making comments on infra-generic classification of Poecilia possible.

Poecilia, Pamphorichthys, Pseudolimia and Limia are considered part of the Poeciliini, whereas Xiphophorus and Priapella are no longer considered closely related to this tribe. Based on the doubtful allocation of Alfaro, this genus is also excluded from the Poeciliini.

Introduction

This chapter designates phylogenetic relationships of all major groups considered related to Poecilia (Table II). In their pre-Hennigian revision of the Poeciliidae, Rosen and Bailey (1963) lumped many species in doubtful genera, based on overall morphological similarities (Introduction to this thesis). Rosen and Bailey's (1963) characterization of the Poeciliini was based on seven basic characteristics (Table I), which are herein used in a phylogenetic analysis (Fig. 1).

Table I. Seven characters defining the Poeciliini sensu Rosen and Bailey (1963).

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>All members have a short gonopodium (= synapomorphy, not included)</td>
</tr>
<tr>
<td>2</td>
<td>Poecilia and Alfaro share a gonopodial palp, a modified part of tissue connected to gonopodial ray 3 (Character 1: unmodified pelvic fins = 0; modified pelvic fins = 1)</td>
</tr>
<tr>
<td>3</td>
<td>Xiphophorus and Priapella have comparable gonopodia, symbolized here by the presence of a gonopodial blade (Character 2: no palp = 0; small, unmodified palp = 1; large palp = 2)</td>
</tr>
<tr>
<td>4</td>
<td>Xiphophorus and Poecilia share the ability for polymorph color patterns, a character absent in Alfaro and Priapella. (Character 3: gonopodium without blade = 0; gonopodium with blade = 1)</td>
</tr>
<tr>
<td>5</td>
<td>Xiphophorus and Poecilia share similar dentition, i.e., small jaws with delicate compressed teeth (Character 4: three gonapophyses = 0; two gonapophyses = 1)</td>
</tr>
</tbody>
</table>

(Notes and references omitted for brevity.)
Examination of these characters cluster *Xiphophorus* and *Poecilia* in a monophyletic clade, separating these genera from *Priapella* and *Alfaro* (Fig. 1).

Based on non-cladistic data, Rivas (1978) re-elevated *Limia* from subgeneric level (of *Poecilia*) to full generic status. This re-instatement was based on emphasizing the morphological differences, e.g., in the gonopodium, between *Limia* and *Poecilia*, whereas Rosen and Bailey (1963) considered the similarities, e.g., in internal anatomy and only partially in the gonopodium. Rosen (1979) disagreed with the tribal classification of the
Poeciliini, based on a cladistic analysis and split *Xiphophorus* and *Priapella* from the other genera, creating the Xiphophorini. However, his analysis was based on his personal assessment of characters. A similar form of subjective weighting of characters is found in Costa (1991) and Meyer (1993), both workers resurrecting taxa to full generic status, and both using the term "synapomorphies" without providing data matrices, cladograms or evidence for character polarization.

Cladistic papers concerning the Poeciliini were first published on *Xiphophorus*, partially using members of *Poecilia* in their analysis (Rauchenberger et al., 1990; Meyer et al., 1994; Marcus and McCune, 1999). These studies did not result in a resolved cladogram for the genus *Xiphophorus* (cf. Marcus and McCune, 1999) and did not confirm the provisional analysis of Rosen and Bailey (1963; Fig. 1) on the relative position of *Poecilia* (Fig. 2).

![Cladogram of a phylogenetic analysis based on morphological data. Note the resemblance with the analysis of Rosen and Bailey's (1963) data in Fig. 1. *Poecilia* is one of the end taxa of the Poeciliini.](image)

Data matrices and cladograms for the remaining Poeciliini were lacking for *Poecilia* until Rodríguez (1997) produced a phylogeny based on morphological characters, recognizing *Pamphorichthys* and *Limia* as separate genera (Fig. 3). Unfortunately, Rodríguez (1997) did not explain the lack of resolution in his consensus tree, in which the relationship of *Poecilia, Pamphorichthys* and *Limia* could not be resolved. Such a tricotomy might be a reason to unite these taxa again in one single genus. Furthermore, he defined his *Mollies* on the basis of the terminal hooks on the gonopodium and *Poecilia* by the serrae on ray 4a. However, the guppy, *P. reticulata*, possesses both a hook on the gonopodium and has a serrated gonopodial ray 4a, i.e., both of the above diagnostic features, but is regarded a member of the subgenus *Poecilia* (Rodríguez, 1997: 673), thus contradicting his own character assessment.
A further contribution to the classification of *Poecilia* was a molecular phylogeny made by Breden and Ptacek (1998), who constructed a phylogeny of *Poecilia* that superficially indicated monophyly for their *Mollienesia*. Their cladogram, reproduced herein as Fig. 4, suggested that *P. reticulata* was the sistergroup of the Central American mollies.

Breden et al. (1999) attributed the lack of resolution in Rodriguez' (1997) tree to the exclusion of taxa, e.g., "*Poecilia* heterandria (= *Pseudolimia* Poeser, 2002) and the species of *Micropoecilia*. Although Breden et al. (1999), using molecular data, stated that their own analysis "support[s] the subgeneric categories of Rosen and Bailey (1963), with adjustments to the subgenera *Poecilia* and *Pamphorichthys" (Fig. 5), their 'genus' *Poecilia* is also represented by a largely unresolved bush with a polytomy representing the relations between *Poecilia*, *Mollienesia*, *Acanthophacelus* (including *Micropoecilia*), *Limia*, *Pamphorichthys* and *Pseudolimia*. Breden and coworkers (1999) therefore refrained from establishing a taxonomy based on their study and chose to "await a more inclusive study (i.e., including more species and more genera and combining more types of data) ...."
9.1 A phylogenetic analysis of the Poeciliini (sensu Rosen and Bailey, 1963)

Character evaluation of *Poecilia*

*Poecilia* was formerly characterized by two synapomorphies (Rodriguez, 1997), i.e., the presence of a retrorse hook on gonopodial ray 5p, and the dentate serrae located ventrally on gonopodial ray 3 (Figs. 6B&D). However, both these characters are not present in all species.

The members of the *P. vivipara* species group, e.g., *P. vivipara*, *P. koperi*, and *P. vandepolli*, all lack the hook on ray 5p, whereas the Hispaniolan species *P. dominicensis* and *P. hispaniolana* do not have dentate serrae on ray 3. To address this problem, the Panamanian taxa of the *P. sphenops* complex (Chapter 11), viz., *P. gillii"gillii"* and *P. gillii"cuneata"*, are included, as well as representatives of all South American species groups, viz., *P. vivipara*, *P. vandepolli*, *P. koperi*, *P. reticulata*, *P. parae* and *P. caucana*, and the Hispaniolan species *P. elegans* and *P. hispaniolana*. Therefore, the genus *Poecilia* is re-analyzed here on the basis of species formerly considered part of supra-specific taxa and compared to exemplar species for *Alfaro*, *Xiphophorus*, *Platypoecilus*, *Priapella* and *Pseudolimia* (Table 2).
Table II. List of taxa used in the present analysis.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td><em>Alfaro cultratus</em></td>
<td>Exemplar species for the genus <em>Alfaro</em> with unknown relation to <em>Poecilia</em>.</td>
</tr>
<tr>
<td></td>
<td>Included in the Poeciliini by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Brachyraphis roseni</em></td>
<td>Exemplar species for the genus <em>Limia</em>, related to <em>Poecilia</em> in recent</td>
</tr>
<tr>
<td></td>
<td>phylogenetic studies. Subgenus of <em>Poecilia</em> by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Limia vittata</em></td>
<td>Representing a genus related to <em>Poecilia</em> in recent phylogenetic studies.</td>
</tr>
<tr>
<td></td>
<td>Subgenus of <em>Poecilia</em> by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Pamphorichthys minor</em></td>
<td>Exemplar species for the genus <em>Xiphophorus</em> with unknown relation to</td>
</tr>
<tr>
<td></td>
<td><em>Poecilia</em>. Included in the Poeciliini by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Platypoecilus maculata</em></td>
<td>Representing a genus with unknown relation to <em>Poecilia</em>. Included in the</td>
</tr>
<tr>
<td></td>
<td>Poeciliini by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Priapella intermedia</em></td>
<td>Exemplar species for the monotypic genus <em>Pseudolimia</em>, related to <em>Poecilia</em></td>
</tr>
<tr>
<td></td>
<td>in recent phylogenetic studies. Subgenus of <em>Pamphorichthys</em> by Rosen and</td>
</tr>
<tr>
<td></td>
<td>Bailey (1963)</td>
</tr>
<tr>
<td><em>Xiphophorus helleri</em></td>
<td>Exemplar species for the genus <em>Xiphophorus</em> with unknown relation to</td>
</tr>
<tr>
<td></td>
<td><em>Poecilia</em>. Included in the Poeciliini by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia caucana</em></td>
<td>Represents the subgenus <em>Allopoecilia</em>, included in the subgenus <em>Poecilia</em></td>
</tr>
<tr>
<td></td>
<td>by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia elegans</em></td>
<td>Represents <em>Curtipenis</em>, included in the subgenus <em>Poecilia</em> by Rosen and</td>
</tr>
<tr>
<td></td>
<td>Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia gillii “cuneata”</em></td>
<td>Exemplar species for the Central American short-finned mollies, included in</td>
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<td></td>
<td>the subgenus <em>Poecilia</em> by Rosen and Bailey (1963)</td>
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<td></td>
<td>the subgenus <em>Poecilia</em> by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia hispaniolana</em></td>
<td>Represents <em>Psychropoecilia</em>, included in the subgenus <em>Poecilia</em> by Rosen</td>
</tr>
<tr>
<td></td>
<td>and Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia koperi</em></td>
<td>South American molly, not yet included in any phylogenetic study</td>
</tr>
<tr>
<td><em>Poecilia latipinna</em></td>
<td>Represents the sailfin mollies, included in the subgenus <em>Poecilia</em> by Rosen</td>
</tr>
<tr>
<td></td>
<td>and Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia mexicana</em></td>
<td>Exemplar species for the Central American short-finned mollies, included in</td>
</tr>
<tr>
<td></td>
<td>the subgenus <em>Poecilia</em> by Rosen and Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia parae</em></td>
<td>Represents <em>Micropoecilia</em>, included in the subgenus <em>Lebistes</em> by Rosen and</td>
</tr>
<tr>
<td></td>
<td>Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia reticulata</em></td>
<td>Represents <em>Acanthophacelus</em>, included in the subgenus <em>Lebistes</em> by Rosen</td>
</tr>
<tr>
<td></td>
<td>and Bailey (1963)</td>
</tr>
<tr>
<td><em>Poecilia vandepolli</em></td>
<td>South American molly, not yet included in any phylogenetic study</td>
</tr>
<tr>
<td><em>Poecilia vivipara</em></td>
<td>Type species of the genus <em>Poecilia</em></td>
</tr>
</tbody>
</table>

The genus *Brachyraphis* is chosen as out-group, representing a primitive form (cf. Rosen and Bailey, 1963) of another tribe of the Poeciliidae, the Gambusiini. Particulars are taken from the description of *B. roseni* Bussing, 1988 (Fig. 8). Some 27 (of 28) characters are used with the state found in *B. roseni* scored as primitive (= 0) (Table 4). One character, i.e., character 09 (serrated segments on gonopodial ray 4p), is
scored with the absence of segments as "0" (*B. roseni* is here scored "2"). Some 26 characters are treated as unordered, characters 02 and 13 are ordered (see below). Gonopodial characters are either adapted from Rosen and Bailey (1963), Miller (1975), Rosen (1979), Meyer (1993), Rodriguez (1997), mostly based on personal observations. The states of the gonapophyses (Figs. 9 and 10 from the introduction to this thesis, and Fig. 7) are taken from Rosen and Bailey (1963) and Rodriguez (1997). Pelvic fin structures (Rosen and Bailey, 1963; Rodriguez, 1997) are reproduced in the introduction to this thesis (Fig. 8), whereas species descriptions and meristic data are based upon personal observations (Chapters 1 to 8, Appendix 2).

Some 14 characters involve gonopodial structures (figured in most chapters herein). Every ray is scored separately (see especially Fig. 6 of the introduction to this thesis for details), with reference to prior uses and interpretations regarding homologies. In the South American taxa of *Poecilia*, gonopodial appendices are secondary reduced (Hubbs, 1926; Poeser, in press) and are scored accordingly (reduced = 2). These characters (02 and 13) are ordered (0 -> 1 -> 2): it is impossible to change from "absent" to "reduced" (0 -> 2). Three characters (characters 15 - 17) are taken from the gonopodial suspensorium, i.e., the number and angle of the gonapophyses (e.g., Figure 7). The modifications in the pelvic fin provide three more characters (characters 18 - 20, see Figure 8 of the introduction to this thesis). The remaining characters (characters 21 to 28) are morphological and meristic characters, discussed in the character description (see also Appendix 2).

The 28 characters include 13 multistate characters (characters 1, 2, 3, 4, 5, 7, 9, 13, 16, 19, 22, 23, and 26).

Excluded characters
In a preliminary survey, some possible characters were reviewed and excluded from the data matrix. These characters included size (large versus small species), which was excluded because small species occur only in South America, suggesting a strong geographical correlation. Size is, therefore, considered to be strongly influenced by ecological factors, and not reflecting phylogenetic relationships. The number of scales around the caudal peduncle is strictly correlated to size, viz., all small species have 14 scales around the caudal peduncle and larger species 16 or 18 scales around the caudal peduncle. Based on the same argument, this character is, therefore, excluded.

The analysis was performed with PAUP, with the following specifications:
Addition sequence: simple; # Trees held at each step: 1; Swapping algorithm: TBR; Collapse option in effect: yes (max); Multrees option in effect: yes; Steepest descent: no; Keeping tree in score ≤ N/A.
Figure 6 (After Rosen and Bailey, 1963). Gonopodial tips of the species of the Poeciliini. A) Alfaro cultratus; B) Poecilia (Poecilia) latipinna; C) Poecilia (Psychropoeocilia) hispaniolana; D) Poecilia (Acanthophacelus) reticulata; E) Pamphorichthys minor; F) Limia vittata; G) Xiphophorus helleri; H) Priapella intermedia.
From the Amazon river to the Amazon molly and back again: Chapter 9

Figure 7 (After Rosen and Bailey, 1963). Skeletons of the Xiphophorini sensu Rosen (1979)
A) Priapella; B) Xiphophorus

Figure 8 (After Bussing, 1988). Characteristics of Brachyraphis roseni.
A) Gonopodial suspensorium; B) Gonopodium with all rays numbered
Table III. Description of the characters used in the present analysis.

01. Gonopodial palp.
State 0 = absent
State 1 = extending to tip
State 2 = extending beyond tip
The gonopodial palp is a fleshy structure, ventrally attached to the third gonopodial ray (Fig. 3.2A-F). When present, it extends to the gonopodial tip. The reduced size in *P. dominicensis* is not considered. In *P. reticulata* the palp extends clearly beyond the tip, which modification is scored as "2". In some genera that do not have this structure, e.g., *Xiphophorus* and *Pseudolimia*, a membranous thickening of the third gonopodial ray is present, which might be a homologous structure. The presence of this tissue is not considered and therefore also the absence of this structure in *P. elegans* is scored as "0".

The gonopodial palp is present in a closely related group of genera, the Poeciliini sensu Hubbs (1926). It is also found in *Alfaro*, which genus was therefore considered part of the Poeciliini by Rosen (1979). Based on a multifold of deviating morphological characters, *Alfaro* was removed from the Poeciliini (Ghedotti, 2000).

02. Membranous hook ventrally on gonopodial ray 3.
State 0 = absent
State 1 = present
State 2 = secondary lost
The rays of the gonopodium show specialized developments (Rosen and Bailey, 1963), e.g., the 3d, 4th and 5th anal fin rays thicken and form serrae and hooks. The hooks extrude at the tips, the serrated structures are found internally on the segments on different rays. The characteristic ornamentations provide excellent characters in taxonomic studies (Regan, 1913; Hubbs, 1926), which were largely ignored by Rosen and Bailey (1963).

The membranous hook on ray 3 is secondary lost in the South American species of *Poecilia* (cf. Poeser, in press), even reduced from "normal" to "absent" within a single species, viz., *P. gillii* "gillii" and *P. gillii* "cuneata". In other species of *Poecilia*, e.g., *P. reticulata, P. caucana,* and *P. parae*, the hook also (partially) absent. There is no doubt that these taxa are closely related, and therefore the lack of one or more hooks is considered a secondary loss. This character is "ordered": the hook can only reduce after being present, cannot change from "0" to "2". The absence of a hook in *P. elegans* is herein scored as "0".

03. Gonopodial blade.
State 0 = absent
State 1 = present, but membranous
State 2 = ossified
Like character 2, some species have an extrusion ventrally at the tip of ray 3. This tip is supported by a membranous or bony structure, the gonopodial blade (Rosen, 1979; Rodriguez, 1997). The presence of this structure is disputed by Rodriguez (1997). It is here considered present in *Priapella* and ossified in *Xiphophorus*, but (as a compromise) not as homologue structure and, therefore, not ordered.

04. Position of serrae on gonopodial ray 3.
State 0 = absent
State 1 = ventrally present
State 2 = bilaterally present
There is considerable variation in the shape and position of the serrated structures of the subdistal segments on ray 3. The incongruous structures found in *Pamphorichthys* are scored as "bilateral", all other structures as "ventrally present". The variation in shape is elaborated in character 5.

05. Shape and number of serrae on ray 3.
State 0 = unmodified
State 1 = less than nine, spiny serrae
State 2 = 10 or more, spiny serrae
State 3 = elongated and bent processes
Unmodified segments, i.e., rectangular or slightly T-shaped, are found in *Brachyraphis* and *Alfaro* (cf. Rosen and Bailey, 1963; Rodriguez, 1997). Most species of *Poecilia* have spiny serrae. Notable exceptions are seen in *P. dominicensis* and *P. hispaniola*, which have T-shaped extrusions,
and in *P. reticulata*, which has many, elongated and strongly bent serrae. The latter structures were scored formerly "comb-like" (Meyer, 1993). In *Xiphophorus* and *Platypoecilus* the spiny serrae are elongated and bend (= 3).

06. Serrae dorsally on ray 4a.
State 0 = absent
State 1 = present
The 4th gonopodial ray is split into an anterior ray and a posterior ray, 4a and 4p. In three species, *P. vivipara*, *P. reticulata* and *P. picta*, small bulbs are found dorsally on ray 4a (cf. Fig. 6).

07. Shape of segments in gonopodial rays 4a and 4p.
State 0 = in 4a deeper than long
State 1 = in 4p deeper than long
State 2 = cubicule in both rays
When the subdistal segments in ray 4a or in 4p are deeper than long (cf. Fig. 6 of the introduction to this thesis), this ray seems thicker than the other (Rosen, 1975; Rauchenberger, 1988; Poenser, in press). Gonopodial ray 4a is thicker in *Brachyraphis* and is therefore scored as '0'. Gonopodial ray 4p thicker than 4a (= 1) was a character suggesting phylogenetic relations between *P. caucana* and the genera *Limia* and *Pamphorichthys* (cf. Rosen, 1975; Rauchenberger, 1988).

08. Lengths of gonopodial rays 4a versus 4p.
State 0 = ray 4a is equally long as 4p
State 1 = ray 4a longer than 4p
In most taxa, these rays are of equal length. The shapes of the tips of *Priapella* and *Xiphophorus* are similar, expressed here as an unambiguous character.

09. Serrated segments on gonopodial ray 4p.
State 0 = absent
State 1 = present anteriorly to more than 14 unserrated distal segments
State 2 = present anteriorly to 1 - 13 unserrated distal segments
State 3 = all distal segments are serrated
The distal segments in ray 4p differ in slightly in shape, but show constant variation in number of serration. These numbers are clear-cut, but blur the infrageneric differences in *Poecilia*, within which all values are between 1 and 13.

10. Serrae on gonopodial ray 5a.
State 0 = absent
State 1 = present
Ventral extrusions on ray 5a form a keel, connecting rays 4 and 5. Rodriguez (1997) used this character as a synapomorphy for *Limia*, *Pamphorichthys* and *Poecilia*. Investigation of the gonopodia of *Acanthophacelus*, *Micropoecilia* and several species of *Limia*, however, showed this character to be absent.

11. Shape of gonopodial ray 5.
State 0 = (nearly) straight
State 1 = abruptly bend to gonopodial ray 4
Most species have a nearly straight gonopodium. In *Limia* ray 5 is bend to ray 4, aided by a membranous structure (Rosen and Bailey, 1963; Rivas, 1978, 1980; Rodriguez, 1997). The deviation in *Xiphophorus* is considered to originate by the formation of a hook on ray 5a (character 12).

12. Hook on ray 5a.
State 0 = absent
State 1 = present
The last segment of gonopodial ray 5a is sometimes thickened and bends, forming a dorsal hook on the gonopodium. Because the gonopodium of *Priapella* is missing the section of the gonopodium where this hook should be, this character is scored as a question mark.

State 0 = absent
State 1 = present
State 2 = lost
Like characters 2 and 12, a retrorse extrusion can be found at the distal end of ray 5p. In the *P. vivipara* species group (cf. Poenser, in press), this character is considered secondary lost (see also character 2). This character is "ordered": the hook can only reduce after being present, it cannot change from "0" to "2".
14. The length of gonopodial ray 5a versus length of gonopodial ray 5p.
State 0 = (nearly) equal
State 1 = gonopodial ray 5a extends 6 segments or more from gonopodial ray 5p
In the species that have a hook on ray 5, the rays 5a and 5p are of equal length. In the species that do not have a hook on this ray, 5a is longer than 5p, with the exception of the P. vivipara species group and P. parae. This character therefore confirms the suggested secondary loss of the hook in the latter groups of species.

15. Number of gonapophyses
State 0 = 3
State 1 = 2
Gonapophyses are modified ribs, projecting downwards to support the gonopodium. In most species of the Poeciliidae, the number of gonapophyses is 3 or 4, whereas the species of Poecilia sensu Rosen and Bailey (1963) have two. In Alfaro, both 2, 3 and 4 gonapophyses are found (Rosen and Bailey, 1963).

State 0 = perpendicular
State 1 = bent forward
State 2 = parallel to spinal cord
The angle of the gonapophyses is mildly correlated to the number of gonapophyses, i.e., three gonapophyses are mostly perpendicular. In the genus Priapella (cf. Rodriguez, 1997), the three gonapophyses seem to bend forward. The gonapophyses parallel to the spinal cord are only found in Pamphorichthys.

17. Ligastyle
State 0 = present
State 1 = small or absent
In most species of the Poeciliidae, a ligastyle is a bony feature, positioned unconnected in front of the gonapophyses. In its most primitive form, it is large (cf. Rosen and Bailey, 1963). In Poecilia sensu Rosen and Bailey (1963), the ligastyle is reduced, with the exception of some species of Limia (cf. Rodriguez, 1997). Also the genus Alfaro seems to have a reduced ligastyle, a fact apparently unnoticed by Ghedotti (2000).

18. Shape of the first ray in the pelvic fin.
State 0 = unmodified
State 1 = elongated
The pelvic fin seems to have a function during courtship and gonopodial use. There is a similarity between the shapes of the pelvic fin in the species of Poecilia sensu Rosen and Bailey (1963) and of Xiphophorus (cf. Rosen and Bailey, 1963; Rodriguez, 1997).

19. Shape of the second ray of the pelvic fin.
State 0 = short
State 1 = elongated without further modifications
State 2 = elongated and modified
In addition to the modifications of the first pelvic fin ray, the second ray can also be modified (Rosen and Bailey, 1963; Rodriguez, 1997). Not only can it be elongated, in Pamphorichthys and Limia it has subsequent modifications. In Limia, this ray is fleshy and curved inward, in Pamphorichthys the tip is triangular. The modifications differ in appearance, this character is considered as "the ability to modify" to have possible phylogenetic significance.

20. Shape of pelvic fin ray 3.
State 0 = unmodified
State 1 = distally broadened
In Limia, also the third ray of the pelvic fin is modified, i.e., distally broadened (Rodriguez, 1997).

21. Number of anal fin rays
State 0 = 9
State 1 = 8
In the species that are considered in the present analysis, only two kinds of anal fin numbers are found, sometimes both are found in one species.

22. Number of dorsal fin rays.
State 0 = 9 or 10
State 1 = less than 9
State 2 = 11 or more
In the past, the number of dorsal fin rays was used to distinguish between the species of Poecilia and Mollienesia (cf. Günther, 1866). The lesser
dorsal fin ray numbers (State 1) are mostly found in the South American species.

23. Position of the shoulder spot in females.
State 0 = absent
State 1 = humeral
State 2 = median

A constant pigmentation feature is the presence of a spot on the fore-body in females of certain species. While several species have multicolored males, i.e., *Acanthophacelus* and *Micropoecilia* (character 24), or have body coloration in both sexes, e.g., *Xiphophorus*, only a few taxa have females with a potential shoulder spot, i.e., *P. vivipara* species group and *Micropoecilia*. In *P. vivipara* and *Micropoecilia* the shoulder spot is markedly positioned posteriorly (Poeser, in press).

24. Male body colors
State 0 = absent
State 1 = present

As explained in character 23, males of *Acanthophacelus* and *Micropoecilia* show a remarkable talent for a variegated pattern of red, black, yellow and other spots and stripes on the body and unpaired fins.

25. Relative position of the anal fin in females
State 0 = pre-anal length is about 60% of SL
State 1 = pre-anal length is less than 50% of SL

In most taxa, the anal fin of females is positioned in the hind-part of the specimen. Only in *Alfaro*, the fin is, in addition to its deviating shape, positioned anteriorly. This position, as well as the position of the dorsal fin, highlights the differences in body shape between *Alfaro* and all remaining species presently analyzed.

26. Relative position of the dorsal fin in females
State 0 = less than 50% of SL
State 1 = about 55% to 60% of SL
State 2 = more than 60% of SL

The predorsal length in *Alfaro* (about 65% of the SL) deviated greatly from all other taxa. The large dorsal fin of *Mollienesia* and *Xiphophorus*, however, result in smaller predorsal lengths.

27. Shape of the caudal peduncle.
State 0 = round
State 1 = sharp

The tails of *Priapella* and *Alfaro* are similarly shapes, i.e., sharp. This feature is accentuated by the formation of a scaled keel in *Alfaro*.

28. Shape of the lower margin of the caudal fin.
State 0 = equal to upper margin
State 1 = longer than the upper margin

There is considerable variation in the shape of the lower margin of the caudal fin. Southern swordtails (genus *Xiphophorus*) have the branched fin rays elongated into a sword, as do some species of platyfish (genus *Xiphophorus*, here presented in *Platypoecilus*). Most platyfish, however, do not have a sword at all. In addition to this, the pigmentation in southern swordtails also differs (Marcus and McCune, 1999). Northern swordtails have unbranched caudal fin rays in their swords. In some species of the *P. latipinna* species group (here presented in *Mollienesia*), and in some populations of *P. reticulata*, the lower margin on the caudal might also be elongated.

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**Results**

The cladogram (Fig. 9; consensus of 864 trees, TL = 69, CI = 0.623, RI = 0.737) resolves the intergeneric relations of the Poeciliini and provides some insight to the infrageneric classification of *Poecilia*. The Poeciliini share the gonopodial palp and the reduced ligastyle with *Alfaro*, and modified pelvic fins with *Xiphophorus*. Based on the phylogeny presented herein, these characters are considered homoplasies. The number and shapes of the gonapophyses are true synapomorphies, probably unique in the Poeciliidae.
Infra-generic consequences of the phylogeny (Fig. 9) are discussed in chapter 11, the taxonomy of *Poecilia*.

**Figure 9. Cladogram of the base analysis (consensus of 864 trees, TL = 69, CI = 0.623, RI = 0.737)**
| Poecilia caucana | Poecilia elegans | Poecilia gillii "tuneta" | Poecilia gillii "gilla" | Poecilia kiepioliana | Poecilia kopen | Poecilia latipinna | Poecilia mexicana | Poecilia parae | Poecilia reticulata | Poecilia vandepolli | Poecilia vivipara | Alfero culturatus | Limia vittata | Pamphorichthys minor | Platypoecilus maculatus | Priapella intermedia | Pseudolimia keterandna | Xiphophorus hellen | Brachyraphis rosemi |
|-----------------|-----------------|--------------------------|-----------------------|----------------------|--------------|------------------|------------------|---------------|-------------------|------------------|-------------------|-----------------|-----------------|-------------------|------------------|------------------|------------------------|------------------|
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Table IV. Data matrix of the characters from Table III.
Discussion

The base analysis (Fig. 9) was further examined by analyzing trees one step longer than the most parsimonious tree (Fig. 10; TL + 1 = 70). By looking for consistency in an "one-step-longer-than the base analysis", a more objective analysis of tree topologies is obtained, i.e., more trees are analyzed, minimizing individual errors in tree comparisons. However, some resolution will generally be lost. Constructing a tree one step longer than the base analysis resulted in a 50% majority consensus tree with some resolution, again separating Alfaro from the Poeciliini and separating Poecilia from the remaining Poeciliini. The cladograms recorded herein confirm the generic assumptions of Rosen (1979), splitting the Xiphophorini (Xiphophorus (+ Platypoecilus) and Priapella) from the Poeciliini, viz., Poecilia and Alfaro. In every cladogram, however Alfaro is separated from the remaining genera of the Poeciliini sensu Rosen (1979). I, therefore, follow Ghedotti (2000) in assigning Alfaro in a separate tribe, viz., the Alfarini. The Poeciliini therefore consist of the genera Limia, Pamphorichthys, Pseudolimia and Poecilia. The majority rule consensus tree (Fig. 10) supports the internal relationships of the Poeciliini, as well as the allocations of the species within Poecilia. Again, P. elegans is allocated as the sistergroup of the remaining species of Poecilia, whereas the Central American species of Poecilia, cf. Mollienesia, are superficially separated from the South American species, viz., the P. vivipara species group and P. parae. The latter group is also separated from P. reticulata, implicating different origins for these two species, representing Micropoecilia and Acanthophacelus. These allocations make comparisons with earlier phylogenies interesting.

The phylogeny proposed by Rodriguez (1997; Fig. 3) is fully compatible with the Figure 9. However, this seems due merely because of the lack of resolution in the former phylogeny; his postulated infrageneric relationships, e.g., P. reticulata and P. vivipara are a subgenus separate from Mollienesia, are not supported. The first phylogeny based on molecular data (Ptacek and Breden, 1998) does resemble the phylogeny proposed herein, but has some peculiarities. Ptacek and Breden’s (1998) cladogram shows P. vivipara as one of the basal taxa, whereas it is an end-taxon in Figure 9. Moreover, their cladogram has the South American taxa, viz., P. vivipara, P. reticulata and P. caucana, all as sistergroup of the Central American taxa, whereas the present analysis suggests exactly the opposite. A more detailed examination of their paper revealed that the chose P. reticulata as their outgroup, basically forcing this species to the base of their phylogeny. Re-analyzing their data (Ptacek and Breden, 1998), but now with P. mexicana as outgroup, revealed a surprisingly detailed infrageneric subdivision, closer resembling the phylogeny herein proposed.

Also a final phylogeny, based on molecular data (Breden et al., 1999), is not supported. While their cladogram is largely unresolved, the close relationship they suggested between P. reticulata and P. parae is contradicted in the present study. Moreover, their cladogram proposed equal relationships for all genera and subgroups, herein separated on generic level. This might suggest that the molecular data are more conservative than the morphological data examined in the present study.
The analysis produced at least five synapomorphies for the Poeciliini, being a monophyletic assemblage of *Limia*, *Pamphorichthys*, *Pseudolimia* and *Poecilia* (Fig. 11). The gonopodial palp is present in most species, i.e., is also present in all non-analyzed members of *Poecilia*, lacking in only two species, i.e., *Pseudolimia heterandria* and *Poecilia elegans*. Based on the present cladogram, I consider this character secondary lost in these species. The occurrence of a gonopodial palp in *Alfaro cultratus* is considered a homoplasy. The second character figured, the length of gonopodial rays 5a and 5p, is only absent in *Limia vittata*. Limia, therefore, exhibits the plesiomorph state of this character. Also the states derived from the
internal structures of the gonopodial support, i.e., the gonapophyses and ligastyle (Fig. 11.2), represent synapomorphies for the Poeciliini.

Figure 11.1. Trees showing synapomorphies defining the Poeciliini. A) Character 01, the gonopodial palp. This character is also present in Alfaro, secondary lost in Pseudolimia heterandria and Poecilia elegans, it is relatively long in Poecilia reticulata; B) Character 14, Length of gonopodial ray 5a versus 5b. Of the Poeciliini, only Limia vittata has ray 5a longer than 5b.

Within the Poeciliini, Poecilia is also defined by some synapomorphies, although these characters are not always clear-cut. These characters may represent plesiomorph characters, e.g., the shape of the serrae on gonopodial ray 3 in the Hispaniolan species P. dominicensis and P. hispaniolana, or are either modified or lost, e.g., reduction of terminal hooks on the gonopodia of the South American species, P. vivipara, P. parae, and (in part) P. reticulata. The large range in which Poecilia occurs, i.e., nearly the complete range of the Poeciliini, combined with the geological history of this area (Chapter 10), probably has let to local adaptations of these characters (see Chapter 7), converging character states or make the conservation of plesiomorph states possible, explaining the lack of clear resolution in the cladograms.
Figure 11.2. Trees showing synapomorphies defining the Poeciliini. A) Character 15, number of gonapophyses. All members of the Poeciliini have two gonapophyses versus three in the remaining genera; B) Character 16, the shape of the gonapophyses. The Poeciliini have anteriorly bend gonapophyses, which is extremely forward in Pamphorichthys. This character is shared superficially with Priapella; C) Character 17, the ligastyle is absent or extremely reduced in the Poeciliini, a state which is shared by Alfaro. In Limia, several species have a moderately sized ligastyle, again considered representing the plesiomorph state (see character 14).
Figure 12. Trees showing synapomorphies defining Poecilia. A) Character 02, the presence of a gonopodial hook on ray 3. The presence of a terminal hook in Limia is considered the result of convergence, whereas the hook is secondary absent in several South American taxa, i.e., P. reticulata, P. vivipara, P. vandepolli and P. parae; B) Character 05, shape of the serrae on gonopodial ray 3. Note that P. hispaniolana retained the plesiomorph state, whereas this character is modified in P. reticulata; C) Character 13, presence of a retrorse hook on gonopodial ray 5p. The secondary reduction of this hook is a synapomorphy for the South American mollies and P. parae.
References


